

## THE SURFACE TENSION THEORY OF MEMBRANE ELEVATION.

L. V. HEILBRUNN.

When a sea-urchin egg is inseminated it lifts off a membrane from its surface. A similar phenomenon can be produced by various reagents. Many explanations have been advanced to account for it. Some years ago, I showed that all substances which produce membrane elevation are those which might be expected to produce a lowered surface tension (1). Also, in general, substances which lower surface tension markedly, produce membrane elevation. And so I advanced the view that surface tension lowering was in all cases related to membrane elevation, and I offered a physical explanation of the process based on such a lowering of surface tension. The idea was new, although Traube (2) had previously shown that when substances of a chemical series are compared, those with lower surface tension are relatively more effective in producing membrane elevation. Traube thought the process involved a secretion on return to sea-water.

The surface tension theory of membrane elevation was accepted by some workers (3) but not by others. Garrey (4) in a review of the literature states that the theory demands the existence of a membrane on the uninseminated egg. For this Garrey finds no evidence, and he cites Moore's (5) repetition of Ziegler's (6) and the Hertwigs' (7) experiment with broken-up eggs as an argument against such a membrane. The evidence for a pre-existent membrane is abundantly supplied in my 1915 paper, to which Garrey does not refer.

In a paper published recently, Just (8) claims that hypertonic solutions of sodium chloride in sea-water, which do not lower surface tension, nevertheless produce membrane elevation.<sup>1</sup>

<sup>1</sup> As a matter of fact hypertonic solutions of NaCl in sea-water do secondarily produce lowered surface tension, for they cause membrane swelling and this produces lowered surface tension.

In my 1915 paper, I pointed out that the earlier descriptions of cortical change in the sea-urchin egg had failed to distinguish between two types of cortical change. The normal change at fertilization is a membrane elevation. Many reagents produce this change, others however produce a swelling of the membrane. The two types of change, although fundamentally quite different, are not easy to distinguish morphologically, partly because the surface of the egg is not especially favorable for microscopic observation. I therefore proposed various criteria to distinguish them. Thus elevated membranes collapse in albumen solutions, swollen membranes do not. Other criteria are easily established. When eggs with elevated membranes are crushed, they flatten and obliterate the perivitelline space. Eggs with swollen membranes have little or no perivitelline space, and when they are crushed, the thick membranes remain around them as before.

Just tried none of these criteria. The membranes he describes in his paper seemingly lack a perivitelline space, for he notes that on return to sea-water from the hypertonic solution, the perivitelline space is not obliterated. If the membranes were separated off as Just believes, and if there were a perivitelline space, one would think that this space would be obliterated by the osmotic expansion of the egg on return to ordinary sea-water.

As soon as an opportunity was afforded, I repeated Just's observations. With the concentrations he used (20-24 per cent.  $2\frac{1}{2}$  M NaCl in sea-water), no membrane elevation or separation could be observed. In such solutions the membrane could be seen slowly to expand and swell. There was no evidence at all of a sudden movement of the membrane such as occurs when the membrane is elevated. Tested with albumen solutions the membranes did not collapse. When the eggs were compressed the egg contents did not expand to the outer limits of the membrane. The membranes produced by solutions of sodium chloride in sea-water, or on return from such solutions to sea-water, were certainly swollen and not elevated. In the light of this evidence it appears that the argument advanced by Just is not valid. *It still remains true that all substances which produce typical membrane elevation do in every instance cause a lowering of surface tension.*

It should perhaps be pointed out that in cases of extreme coagulation of the protoplasm, the contents of the egg may sometimes be made to shrink away from the vitelline membrane. No good case of this is known for the sea-urchin egg, although some shrinkage apparently occurs after prolonged heat coagulation. In the *Cumingia* egg, which has a much stiffer membrane than the sea-urchin egg, a membrane which does not normally become elevated, some 1916 experiments showed that the protoplasm would shrink away from the vitelline membrane when the egg contents had been thoroughly coagulated after several hours exposure to hypertonic solutions. Such slow coagulative shrinkages are scarcely to be confused with true membrane elevation, although in the *Cumingia* egg under certain conditions the membrane may become stretched away from the egg after it is released.

Just makes one other point against the surface tension theory. He states that in "the eggs of *Arbacia* and *Echinarachnius* any competent observer can see that membrane separation following insemination is no mere surface tension effect." This is not a very serious argument. The surface tension theory claims only that the lowered surface tension is the cause which underlies the process, not that all the details which follow the initiation of the process are surface tension phenomena. And anyway how can one decide a physical problem by mere visual observation?

Just, apparently, has attempted to do this. The lifting off of the membrane is a physical process and demands a physical explanation. Just's nearest approach to this is his description of membrane elevation as involving a "wave of negativity" (9). But he does not use the word in any known physical sense.

## REFERENCES.

1. Heilbrunn.  
'13 BIOL. BULL., XXIV., 343; 1915, *ib.*, XXIX., 149.
2. Traube.  
'09 Biochem. Zeitsch., XVI., 182.
3. Godlewski.  
Winterstein's Handbuch der vergleichenden Physiologie, III (2), see p. 826.
4. Garrey.  
'19 BIOL. BULL., XXXVII., 287.
5. Moore, A. R.  
'12 Univ. of California Publications in Physiology, IV., 89.

## 6. Ziegler.

'98 Arch. f. Entwicklungsmech., VI., 249.

## 7. Hertwig, O. and R.

'87 Untersuchungen zur Morphologie und Physiologie der Zelle, Heft 5.

## 8. Just.

'22 BIOL. BULL., XLIII., 384.

## 9. Just.

'19 BIOL. BULL., XXXVI., I.